THE MIOCENE VERTEBRATES OF QUEBRADA HONDA, BOLIVIA

PART II. EDENTATA

by

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The uniqueness of the South American fauna is perhaps no better exemplified than by the Edentata. The bizarre body forms attained by some edentates and their near South American endemism have drawn devoted researchers to this group and made the edentates symbolic of adaptive ingenuity in geographic isolation. Edentates are part of the earliest mammalian fauna of South America, the Rio Chico of late Paleocene age (Simpson, 1948). As such, they are a remnant of an early mammalian diversification that either originated or reached and flourished only in South America as that continent drew away from the unified world of the Mesozoic. The earliest known edentate fossils, osteoderms thought to be those of an armadillo, serve little to elucidate the early history of the edentates but do indicate that the two major groups, Cingulata and Pilosa (and perhaps lower taxonomic levels), were already in existence.

By the early Miocene, the lineages were at least broadly defined. Some Miocene genera can be confidently assigned to families that were dominant throughout the Late Tertiary. Others, such as the sloth *Hapalops* discussed here, were insufficiently removed from the common ancestor of the later Tertiary families and cannot be confidently assigned to a Tertiary lineage on present information. The improved fossil record of edentates in the early Miocene reflects the importance of the highly fossiliferous and extensive

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Santa Cruz Formation and the attention it has received from collectors over several decades (Marshall, 1976). From this formation comes a rich mammalian fauna that is dated at 21.7 mya (Evernden et al., 1964, p. 192). This fauna is the basis of the Santacrucian Land Mammal Age and was presumed to typify the early Miocene mammalian fauna of South America (Patterson and Pascual, 1972) despite its restriction to southern Argentina. Other recorded Santacrucian age fossils, in Chile (Hemmer, 1935; Simpson, 1941) and possibly Venezuela (Simpson, 1947), have not added to the definition of this fauna. The hypothesized universality of the Santacrucian Fauna could not be examined for lack of Santacrucian local faunas elsewhere in South America nor could questions of latitudinal and altitudinal influences be meaningfully discussed. With the announcement of the discovery of vertebrate fossils at Quebrada Honda (Hoffstetter, 1977), the known Miocene faunal diversity of South America was expanded and Miocene zoogeography was extended to include a portion of the Cordillera Oriental in southern Bolivia. Among the discoveries at Quebrada Honda are edentates that compare with those in the Santa Cruz Fauna.

The specimens described here were discovered in 1978 by a field party consisting of Dr. K. E. Campbell, Jr. (Los Angeles County Museum of Natural History), Dr. Ronald G. Wolff (University of Florida), Dr. Bruce MacFadden (Florida State Museum), Ing. Oscar Siles (Geological Survey of Bolivia), and the author. Besides the original note by Hoffstetter (1977) and short notes in MacFadden and Wolff (1981) and Takai et al. (1984), only one other paper has been published on this local fauna (Frailey, 1987).

All measurements in this paper are given in millimeters; measurements in parentheses are approximate. The following abbreviations are used: AMNH, American Museum of Natural History; KUVP, Museum of Natural History, University of Kansas; PU, Princeton University; UF, University of Florida/Florida State Museum. The horizon designations, QH1-4, etc., are explained in MacFadden and Wolff (1981) and Frailey (1987).

SYSTEMATICS

Order Edentata Cuvier, 1798
Suborder Xenarthra Cope, 1889
Infraorder Cingulata Illiger, 1811
Family Glyptodontidae Burmeister, 1879
Subfamily Propaleohoplophorinae Castellanos, 1932
Propaleohoplophorus Ameghino, 1887
Propaleohoplophorus andinus new species
Fig. 1

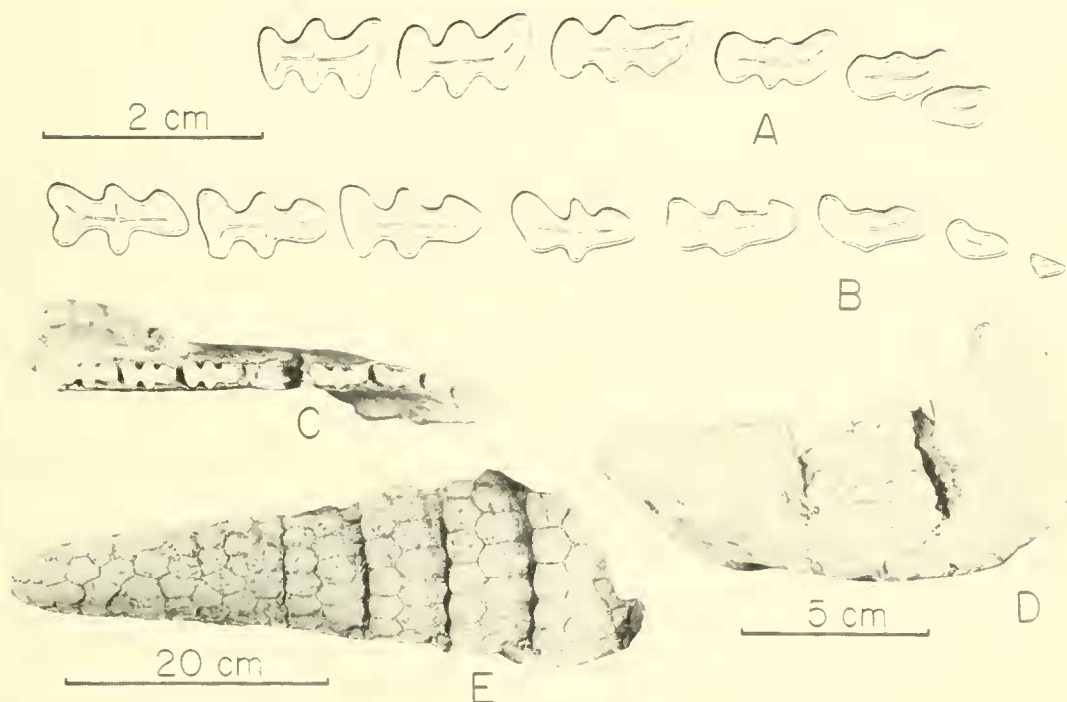Etymology. Pertaining to the Andes Mountains.
Holotype. UF 26677, left ramus.

Fig. 1.—*Propaleohoplophorus andinus* new species. A. UF 26678, right N$^{2-7}$, occlusal pattern. B–D. UF 26677, left ramus, holotype: B. occlusal pattern; C. occlusal view; D. lateral view. E. UF 26676, caudal tube.

Type Locality. QH2-1.

Referred Material. UF 26678, partial skull with N^2-N^7; UF 26671, partial ramus with N$_{5-8}$; UF 26676, partial carapace, hindlimbs, and tail; UF 26673, tip of tail; UF 26672, 26674, 26675, plates of carapace.

Horizons and Localities. UF 26678, QH1-2; UF 26676, QH1-4; UF 26675, QH1-10; UF 26671-3, RR = QH1-2; UF 26674, RR = QH2-3.

Diagnosis. The fourth upper tooth and N$_{3-4}$ more lobate (molariform) than in *Propaleohoplophorus australis*; N^2 overlaps N^3; upper tooth row curves mediad anteriorly. Larger than *P. minor*.

Description. *Upper dentition.*—Dental nomenclature follows Hoffstetter (1958) and Gillette and Ray (1981). The upper teeth are designated N$^{1-8}$. The first upper tooth is not preserved in this sample. The second upper tooth is elliptical in outline but lacks a lingual groove unlike that in *P. australis* (Moreno), 1882 and *P. minor* Ameghino, 1891. The second upper tooth overlaps N^3 approximately 3 mm. The third upper tooth is weakly bilobate labially and trilobate lingually. The anterior part of N^3 turns lingually with no indication of the labial half of the anterior lobes evident in the succeeding teeth. The fourth upper tooth is clearly trilobate with a large anterior lobe that is dominated by the sweep of the medial portion. The anteromedial lobe is the largest lobe on N$^{3-7}$ but becomes proportionally less dominating in the posterior teeth. The posterior lobe is round and poorly defined. In N$^{5-7}$, the anterolateral portion of the anterior lobe increases in prominence toward the posterior of the tooth row until the anterior lobe in N^7 is the largest of the three lobes. A small flexure is developed on the anterior margin as a result of

the expanded lateral half of the anterior lobe. The central and posterior lobes progressively flatten and the posterior margin becomes flatter toward the posterior of the tooth row. The width of the central and posterior lobes is nearly equal with the central lobe being wider. Measurements are as follows (greatest length, greatest width anterior lobe, greatest width posterior lobe in N^{4-7}): N^1 (missing); N^2, 7.2. x 3.7 mm; N^3, 9.9 x 4.3 mm; N^4, 11.8 x 5.2 x 4.6 mm; N^5, 12.9 x 5.3 x 5.2 mm; N^6, 12.7 x 7.4 x 5.9 mm; N^7, 12.2 x 7.7 x 6.0 mm; N^8 (missing).

Lower dentition.—Lower teeth are designated N_{1-8}. The first lower tooth is small, bean-shaped, with a slight lateral flexure. Length x width of N_1 is 3.6 x 1.8 mm. The second lower tooth is more elongate than N_1 but otherwise very similar. The lateral flexure is placed more posteriorly than in N_1 and anticipates the posterolateral reentrant (fold between the central and posterior lobes) in the following teeth. Length x width of N_2 is 6.7 x 2.6 mm. The third lower tooth has the laterally concave flexure of N_{1-2} and the first indication of a central lobe. Length x width of N_3 is 10.6 x 4.2 mm.

The development of N_{4-8} is similar and these teeth will be discussed together. N_{4-8} are placed on the straight portion of the ramus unlike N_{1-3} which sit on that part of the ramus which curves toward the symphysis. The longitudinal axes of N_{4-8} are thus straight (with a very slight curve in N_4). In contrast to the upper teeth in which the medial portion of the anterior lobe is the most prominent occlusal feature and points anteromedially, the lateral portion of the posterior lobe of each lower tooth is highly developed and points posterolaterally. These lobes correspond to the less expanded portions of the complementary teeth (occluding teeth) and provide a wide, diagonal grinding surface that passed over a smaller surface. This conformation brings the edges into use with a shallower lateral chewing stroke than would be necessary with two equally broad surfaces. In this respect, the anterior lobe is small in N_{4-8} in that the medial portion of the anterior lobe does not develop in this species and the anterior margins of the teeth are rounded. This anterior margin might be interpreted as the missing medial portion in that the lateral portion exists well posterior to the anterior tooth margin and the central axial plate of osteodentine extends into this rounded end as it does into each of the other lobes. Also, the medial portion of the posterior lobe, which increases in size from N_4 to N_8, alters its position relative to the lateral portion and points posteromedially rather than medially.

Measurements of N_{4-8} from the holotype (UF 26677) are as follows (greatest length, greatest width anterior lobe, greatest width posterior lobe): N_4, 13.0 x 4.0 x 4.8 mm; N_5 (12.3) x (3.8) x 5.6 mm; N_6, 13.5 x 4.6 x 7.0 mm; N_7, 12.6 x 4.2 x 6.3 mm; N_8, 13.2 x 4.2 x 5.5 mm. Measurements of the referred ramus (UF 26671) are: N_5, — x — x 6.0 mm; N_6, 15.6 x 4.5 x 5.8 mm; N_7, 15.6 x (4.7) x 5.8 mm; N_8, 14.6 x 4.9 x 4.8 mm.

Mandible.—The rami are straight and parallel between N_{4-8} and only approximately 20 mm apart for this distance. Anterior to N_1 the alveolar margin of the mandible broadens and is pitted. From the lateral aspect, the ramus presents a smooth ventral curve of increasing radius from below N_8 to the anterior of the ramus. The lower extent of the symphysis is beneath a point

between N_3 and N_4. Three mental foramina are present on UF 26677 (left ramus): the largest near the center of the symphysis, a smaller one behind the first and below N_2, and the smallest higher than the first two and situated beneath N_3.

Measurements of the mandible are as follows: N_{1-8} length, 99.6 mm; depth below N_3 including symphysis, 34.8 mm; depth below N_6, 39.7 mm (holotype) and 44.0 mm (UF 26671).

Body armor.—The osteoderms are highly variable and undiagnostic. Genera based on plates alone are probably not valid (Porta, 1962). The tail of *Propaleohoplophorus* is imperfectly known, but a partial carapace with tail (UF 26676) was found at Quebrada Honda. In this specimen, the anterior portion of the tail consists of four and possibly five concentric rings which decrease in diameter toward the posterior. Each ring is composed of two circlets of plates. The anterior circlet is composed of rectangular plates (posterior end round or bifaced) in which the anterior half of each plate lacks a pattern and in which the surface is lower than in the posterior half. The anterior half slides beneath the preceding caudal ring and permitted movement of the tail. The posterior half of the plates in the anterior circlet of each caudal ring has the remnants of the pattern seen in plates of the carapace in that there is a central circle and peripheral circles but the latter are present only towards the anterior. The plates in the posterior circlet of each caudal ring are the reverse of the anterior plates in outline but are shorter, patternless, and without an area of the plate that is depressed.

The plates in the caudal tube are irregularly shaped, generally hexagonal, and maintain approximately the same size throughout the length of the tube. There are no large plates at the tip. The plates lie in uneven lines over the length of the tube. The caudal tube itself decreases in size posteriorly and terminates in a single rounded tip.

Discussion. *Propaleohoplophorus* is the most common of five genera of Glyptodontidae in the Santa Cruz Fauna (Scott, 1903). Thus far, it is the only genus of glyptodont found at Quebrada Honda and is relatively abundant. In dental features, *Propaleohoplophorus andinus* is advanced with regard to the Santacrucian species and indicates a slightly younger age for the Quebrada Honda local fauna. *Propaleohoplophorus* has extensive temporal and geographic ranges, as it is also found in the La Venta local fauna of Venezuela (Porta, 1962) although the fragmentary nature of the specimens there precludes other than generic identification.

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Infraorder Pilosa Flower, 1883
Superfamily Megalonychoidea Simpson, 1931
?Family Megalonychidae Zittel, 1892
Hapalops Ameghino, 1887
Hapalops angustipalatus Ameghino, 1891
Fig. 2

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Referred Material. UF 26668, partial skull, mandible, limb fragments.
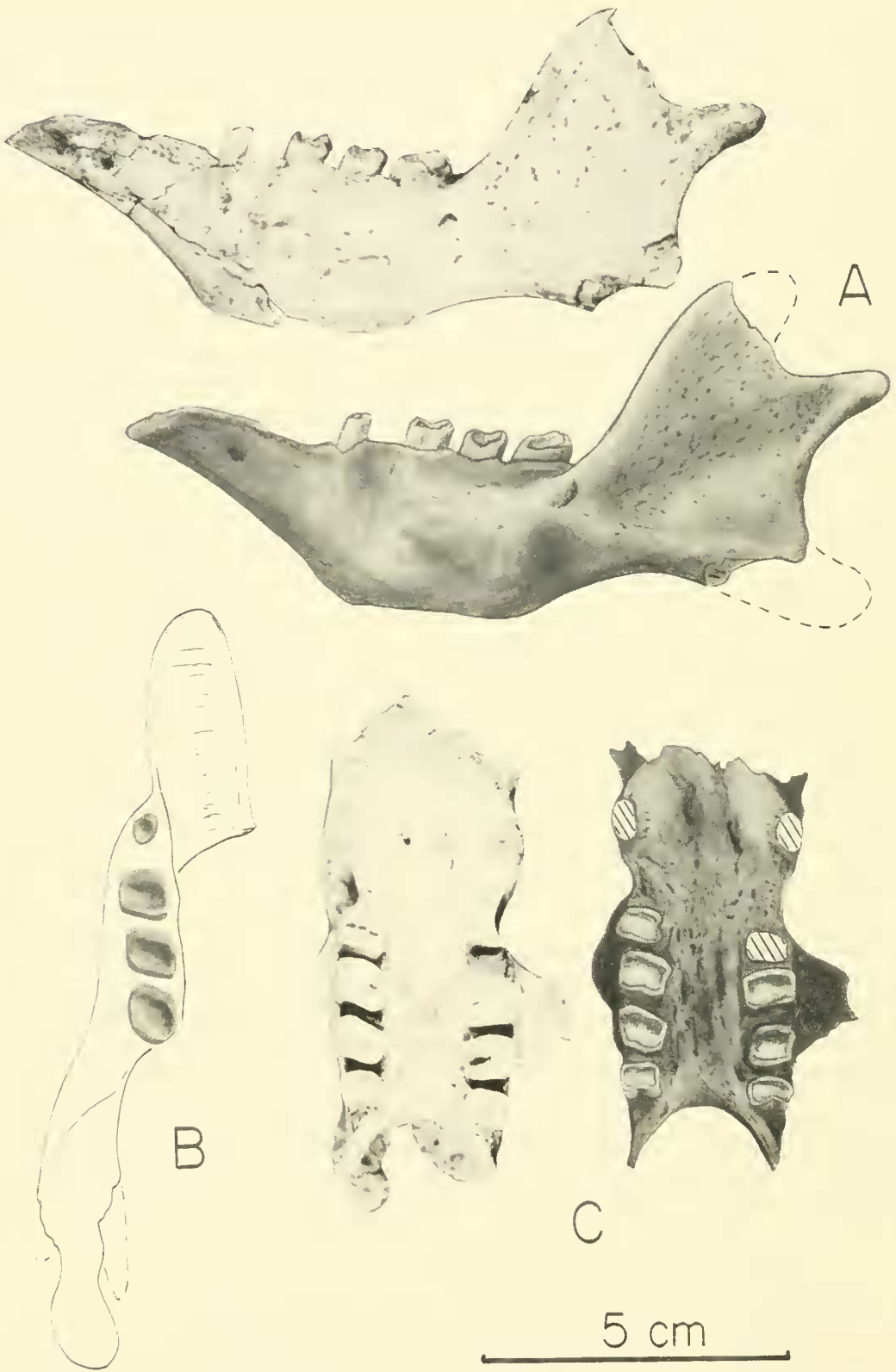**Horizon and Locality.** QH1-4.

Fig. 2.— *Hapalops angustipalatus*. UF 26668. A. left ramus, lateral view, photograph and drawing. B. left ramus, occlusal view of teeth and outline drawing of ramus. C. palate, photograph and drawing.

Description. *Upper dentition.*—The five upper teeth are designated M^{1-5} in this paper. The first upper tooth is caniniform, nearly oval in cross-section with a flattened medial side. In UF 26668, M^1 did not occlude with M_1, possibly an individual variation, and consequently formed a central wear pit instead of a slanted shear facet. The M^1 of UF 26668 is 6.2 x 4.2 mm (length x width). The alveolus of M^1 is 7.1 x (5.3) mm.

The occlusal outlines of M^{2-4} are trapezoids with the shorter of the two parallel sides to the anterior on M^2 and toward the posterior in M^{3-4}. The anterior and posterior margins of M^{2-4} are slightly convex to the anterior. In M^{2-4} and M^1, the labial portion of the anterior rim is the highest point on the tooth. Transverse valleys are well formed in M^{2-4}, although best expressed in M^2, becoming progressively more of an enclosed oblong pit toward the posterior of the tooth row. The latter feature results from wear which does not proceed across the transverse valley beyond the boundaries of M^{3-4} as definitively as in M^2. The exits of the transverse valleys of M^{3-4}, particularly M^4, are therefore more shallow and V-shaped than is seen in M^2. The second through fourth upper teeth are straight in lateral view although positioned in the skull such that they exit with a slight, perhaps 10°, tilt to the anterior. Measurements of greatest length x greatest width for M^2, M^3, and M^4 are as follows: 6.0 x 7.7 mm; 6.4 x 9.1 mm; 6.2 x 8.4 mm.

The fifth upper tooth is rectangular in occlusal outline with a longitudinal groove extending down the posterior side. The occlusal surface is essentially a single plane with only a remnant of the anterior tooth margin extending above this surface to form a small transverse valley. In lateral view, M^5 is curved to the anterior with the posterior rim of the occluding surface below the center of the alveolus. Greatest length x greatest width of M^5 is 4.6 x 6.8 mm.

Primary wear facets are on the internal margins of M^{2-4}, the anterior external margins of M^{3-4}, and the posterior external margins of M^{2-3} with lesser but still plainly evident wear on M^4.

Skull.—Only the palate, maxillaries, and a portion of the basicranium are preserved in UF 26668. The tooth rows are straight and parallel medially but slightly convex laterally because of the greater widths of M^{3-4}. M^1 is separated from M^2 by a large diastema (13.5 mm). The palate narrows at the diastema with large buccinator fossae present on each side of the maxillae. The lateral margin of the alveolus for M^1 equals the greatest lateral extent of the rest of the tooth row (at M^3). The maxillary palate extends 6.3 mm anterior to M^1. The palate is rugose, pitted, and slightly convex, 2 mm below the alveoli of M^{2-5}. The postpalatine notch is broadly rounded and reaches forward to the posterior border of M^5.

Measurements of the skull are: nasal length, 55.7 mm; post-palatal length, (70) mm; palatal width at M^1, (31) mm; at M^5, (27) mm; M^{1-5}, 50.2 mm; M^{2-5}, 29.3 mm.

Lower dentition.—The lower teeth are designated M_{1-4} in this paper. The first lower tooth is caniniform and recurved to the posterior. It is nearly oval in occlusal outline with a flat surface medially. The long axis of the occlusal outline is directed anteromedially at a 45° angle to the remainder of the tooth

row. As in the corresponding upper tooth, M_1 has a pit rather than a diagonal shear plane developed through ware. The greatest length x greatest width of M_1 is 5.4 x 3.8 mm.

The second and third lower teeth are trapezoidal in occlusal outline with the shorter of the parallel sides to the anterior. The center of each tooth wears more than the margins with the result that the transverse valley of each is bounded by shallow, V-shaped lateral walls. The $M_{2,3}$ are slightly recurved. The highest point of each tooth is the lingual side of the posterior edge. Measurements of $M_{2,3}$ (greatest length x greatest width) are 6.8 x 8.8 mm and 6.9 x 8.9 mm.

The M_4 is teardrop-shaped in occlusal outline with the point placed anterolabially. There is no transverse wear valley as in $M_{2,3}$ but rather a shallow, inclined central pit that exists as a small cleft at the point of the occlusal teardrop and has its highest part, as does the tooth itself, at the posterolingual point of M_4. The M_4 is more posteriorly inclined than $M_{2,3}$. The length x width of this tooth in occlusal position is 9.3 x 8.6 mm.

Primary wear facets are on the internal and posterior external margins of M_{2-4} with lesser wear facets developed on the anterior external margins.

Mandible.—The lower tooth rows were apparently parallel although in UF 26668 these are now distorted and this feature is not certain. The first lower tooth lies in the midline of the tooth row and is separated from M_2 by a short diastema (4.2 mm). There is a small fossa labial to the diastema. The ramus maintains a uniform depth beneath M_{1-4}. Immediately anterior to M_1 the upper margin of the ramus rises in a low, dorsally convex curve toward the anterior extremity. The lower margin rises sharply in a shallow, ventrally concave curve toward the anterior extremity. The ascending ramus, horizontal ramus including the tooth row, and the narrow predentary snout are arranged in three parallel, vertical planes. The postdental portion of the ramus has the typical trifid shape with the coronoid and angle of equal size and symmetrically placed about the condyle. The medial surface of the coronoid is excavated and lightly rugose at the insertion of the external pterygoid muscle. This is evidently highly variable and indicates different strengths of that muscle among individuals. The mental foramen is placed well forward on the mandibular spout about half the distance between the anterior mandibular margin and M_1. The mandibular foramen (inferior dental foramen) is centrally situated in the ascending ramus level with the alveolar row. The posteroexternal opening of the posterior mandibular foramen (dental foramen) is placed lateral to the dorsal edge of the ascending ramus at the posterior extent of M_4.

Discussion. The last major treatment of *Hapalops* Ameghino, 1887 (Scott, 1903, 1904) lists 37 species of this genus in the early Miocene Santa Cruz Formation of Argentina. This appears to be excessive splitting, particularly in view of the near contemporaneity of the fauna (Marshall, 1976), but indeed represents about a 50% reduction in species names that were in use before 1904. Scott (1932, p. 205) was also aware of this unlikely taxonomic division of *Hapalops* and attributed the confusion to the remarkable variability of individuals (no two are alike) and to the lack of stratigraphic information with

the fossils. The ensuing years have not corrected this situation and such a work is beyond the scope of this study. A review of the species assigned to *Hapalops*, using modern statistics of populations, would surely provide a more realistic distribution of species in the early Miocene.

The length of the mandibular spout and the long, narrow skull place this species among a series of other *Hapalops* species: *H. elongatus* Ameghino, 1891; *H. rostratus* Ameghino, 1887; *H. atlanticus* (Ameghino), 1891; *H. ruetimeyeri* Ameghino, 1891; *H. gracilidens* Ameghino, 1891; and *H. angustipalatus* Ameghino, 1891 (Scott, 1904, p. 261). On the basis of a close similarity of the upper dentition of *Hapalops angustipalatus* and the specimen from Quebrada Honda, the species of *Hapalops* found at Quebrada Honda is considered conspecific with the Santa Cruz species *H. angustipalatus*. This similarity extends to the size, position of caniniform teeth, and the distinctly trapezoidal molariform teeth. Although not mentioned as significant by Scott (1904), the Quebrada Honda species shares the position of the posteroexternal opening of the dental foramen and the posterior groove on M^5 with a referred specimen of *H. angustipalatus* (PU 15342).

The mandible of *H. angustipalatus* was previously unknown. However, a partial mandible in the KU collection, KUVP 11618 from the Río Gallegos of Argentina, is indistinguishable from that associated with the partial skull of *H. angustipalatus* from Quebrada Honda and undoubtedly referable to this species.

Hapalops angustipalatus is one of the better defined species of *Hapalops* although a future study may synonymize this and many other *Hapalops* species. The correlation between Santa Cruz and Quebrada Honda faunas as evidenced by this species will remain valid in any event.

PHYLETIC RELATIONSHIPS

The generic diversity of Santacrucian ground sloths is great and all bear a general resemblance even though the three major families are already delimited. In the Mylodontidae Gill, 1872, *Nematherium* Ameghino, 1887 and *Analcitherium* Ameghino, 1891 both show the closely placed teeth, the sequential anteromedial rotation of the tooth axis toward the anterior of the tooth row, the lobation of M_4, and the even decrease in depth of the rami toward the anterior which are to be seen in all later genera with the single exception of a new genus from Huayquerian deposits in the Peruvian Amazon (Frailey, 1986.). Only the lobation of M_4 (weak lobation of M^5 in later genera such as *Glossotherium* Owen, 1840) and the orientation of the tooth axes are in contrast to features seen in the Oligocene genera *Orophodon* Ameghino, 1895 and *Octodontotherium* Ameghino, 1895 which apparently form an early derivation of lobate teeth, but, as Hoffstetter (1956) points out, are unrelated to the Mylodontidae and should not be considered as the first representatives of this family to appear in the fossil record (Patterson and Marshall, 1978).

Megatheriidae Owen, 1843 is represented by *Planops* Ameghino, 1887 and *Prepotherium* Ameghino, 1891 in Santacrucian deposits. These genera are the largest ground sloths in the Santa Cruz Fauna and foreshadow the

features of *Megatherium* in shape of skull, mandible, and astragalus although the shape and position of the teeth are little differentiated from other Santacrucian genera. The characteristic, closely spaced teeth and strong, parallel anterior and posterior tooth margins are all post-Santacrucian developments in the Megatheriidae.

Planops and *Prepotherium* clearly belong in the Megatheriidae but *Hapalops* does not. The occasional placement of *Hapalops* in this family (e.g., Savage and Russell, 1983) apparently follows the presumed relationship between this genus and the Nothrotheriinae Kraglievich, 1923 and the placement of this subfamily in the Megatheriidae (e.g., Paula Couto, 1971). This relationship is largely based on overall similarity that includes many features that are consistently primitive in the Nothrotheriinae and, therefore, far from conclusive. There is also no agreement on the familial placement of the Nothrotheriinae (Megalonychidae to some authors, e.g., Simpson [1945, 1980] and Pascual [1968]). In this paper, I have retained the conservative classification for *Hapalops* (that of Scott [1903, 1904] and Simpson [1945]) but question the appropriateness.

The Megalonychidae are represented by *Eucholoeops* Ameghino, 1887 and *Megalonychotherium* Scott, 1904 with their strongly caniniform anterior teeth and short, deep mandibles. Again, the features of the individual teeth are remarkable only in their similarity to all the non-mylodont genera: *Planops*, *Prepotherium*, and *Schismotherium* Ameghino, 1887; *Pelecyodon* Ameghino, 1891; *Hapalops* and *Analcimorphus* Ameghino, 1891. Clearly, all these genera reflect the proximity of their phyletic relationship. *Planops* and *Prepotherium*, as stated earlier, are placed in the Megatheriidae and the other genera are grouped in the Megalonychidae with *Eucholoeops* and *Megalonychotherium*. This latter arrangement is unsatisfactory because it is based only on gross similarity and on the absence of more highly characteristic features of the Mylodontidae and Megatheriidae. Since *Hapalops*, *Schismotherium*, *Pelecyodon*, and *Analcimorphus* share no derived features with *Eucholoeops* or *Megalonychotherium*, their placement in the Megalonychidae is misleading. Polarities cannot now be demonstrated for any of the characters of *Hapalops*, *Schismotherium*, *Pelecyodon*, or *Analcimorphus* and their relationship to the unmistakable megalonychids, *Eucholoeops* and *Megalonychotherium*, as well as to *Planops* or *Prepotherium*, true megatheriids, cannot be demonstrated. It may prove more reasonable to place these four genera *incertae sedis* within the superfamily Megalonychoidea Simpson, 1931 rather than suggest that affinities are readily apparent with other genera of the Megalonychidae.

CONCLUSIONS

The Edentata of Quebrada Honda display taxonomic similarity to the Santa Cruz Fauna as well as differences in diversity. The single recognized species of ground sloth, *Hapalops angustipalatus*, apparently occupied a range that encompassed much of today's Patagonian Faunal Subregion (Hershkovitz, 1972) during the early Miocene. This species is indistinguishable from a species in the Santa Cruz Fauna. However, numerous species of

Hapalops have been named in that fauna and only one has been identified at Quebrada Honda.

The new species of glyptodont, *Propaleohoplophorus andinus*, on the other hand, is relatively more advanced than species of this genus in the Santa Cruz Fauna. For this reason, Quebrada Honda may prove to be slightly younger than the greater portion of the Santa Cruz Fauna. In this respect, it would be interesting to compare the Quebrada Honda local fauna with the Santacrucian local fauna of Lake Pueyrredon which also may be slightly younger in age than the majority of the local faunas in the Santa Cruz Formation (Scott, 1932). Unfortunately, there are only a few taxa known from Lake Pueyrredon and none of these is comparable to members of the Quebrada Honda local fauna.

A further note on the Edentata of the Quebrada Honda local fauna is the apparent paucity of this order in both species diversity, as mentioned in connection with *Hapalops*, and in higher taxonomic groups. Tatuidae, Peltephilidae, and Megatheriidae are absent from Quebrada Honda collections. The Mylodontidae are included by Takai et al., (1984) on the basis of one fragmentary tooth that is unidentifiable below the family level and may not be correctly referred at that. Also, among the Glyptodontidae, only one genus is present in contrast to five at Santa Cruz. Among the Megalonychidae, only the one genus (*Hapalops*) is present as compared to seven genera at Santa Cruz. This is a marked reduction that probably reflects real differences in taxonomic abundances, and not simply collector bias, as three different expeditions have failed to improve on the recorded diversity.

ACKNOWLEDGMENTS

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